

# Fast orienting movements to visual targets: Neural field model of dynamic gaze control

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**Abstract.** The neural machinery in the superior colliculus and the brain stem of primates is responsible for *overt orienting* in the form of saccadic eye movements. High-level principles of neural computing underlying saccade control such as neural mapping, population coding and processing in layered systems are applied to formulate a double-layer *neural field model* of the SC motor map. A key feature of this model is that short-term memory of target location and dynamic gaze control in the motor map has been realized through the nonlinear, spatio-temporal dynamics of neural populations organized in neural fields. The various activity patterns observed in the two layers of the motor map suggests specific schemes of lateral interconnections within these map layers.

## 1. Introduction

Traditionally, information processing tasks have been analyzed on discrete levels [4]. The present work is part of an attempt to integrate findings obtained by behavioral, neurobiological and computational studies on the oculomotor system of primates. The neural machinery which underlies *overt orienting movements* is realized in the superior colliculus (SC) and the brain stem of primates. Functional considerations [3] and recent neurobiological results [7] suggest a 3-compartment model corresponding to (1) the retinotopic transformation of visual input, (2) the selection of a target and the programming of a saccade and (3) the dynamic coding and control of the gaze trajectory. In the following, we restrict our attention to functions of the second and third compartments.

The SC is part of a system extending from cerebral cortex to the brain stem that controls the generation of saccades [12]. Whereas the upper SC layers contain a retinotopic map of the visual hemisphere, the deeper layers host a motor map of rapid eye movements (saccades) [11]. That is, the location of active neurons in the deep layers represents the vector of motor error, i.e.

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the amplitude and direction of the saccade to reach the target. The range of possible saccades prior to which a given neuron discharges defines its movement field (MF) while the neuron is firing for a specific but large range of movements. The topography of the motor map is such that horizontal motor error is encoded mainly along the rostro-caudal axis, and vertical motor error along the medio-lateral axis. The more caudal (medio-lateral) the center of activity is located, the larger the horizontal (vertical) motor error.

A population of saccade neurons starts firing when a motor error occurs, where the activity distribution within the motor map looks like a bell-shaped hill. Saccades to different parts of the visual field are preceded by activity hills in different regions of the map.

A recent study on the collicular dynamics in rhesus monkeys [7] has identified three types of SC neurons with different activity patterns. There are two types of movement-related cells, i.e. burst neurons (BNs) and buildup neurons (BUNs). The activity in the BN layer is maximal at the saccade onset and declines during movement as the motor error decreases while not spreading laterally (a hill-flattening effect). The BN activity forms a symmetrical bell-shaped hill. BUNs have a slow buildup of activity in addition to eye movement-related activity. The spatial distribution of activity shows a skewed profile. Activity in the BUN layer seems to travel through the motor map from its initial location towards the fixation zone (a hill-shift effect). The instantaneous hill location on the map specifies the remaining motor error (dynamic error coding). The saccade is terminated when the traveling activity hill reaches the fixation zone. During active visual fixation, the third group of cells, fixation neurons (FNs) increase their discharge. FNs are located in the rostral pole of the SC at a depth similar to that of the BUNs, i.e. they may constitute a subpopulation of BUNs (representing motor error of zero).

These studies suggest how the spatial representation of activity on the motor map is transformed into the temporal code (frequency and duration of discharge) required by motoneurons. The trajectory of activity on the SC motor map seems to spatially encode the instantaneous eye movement motor error signal.

The neural mechanisms by which the collicular motor map might realize this dynamic motor error coding are currently under debate. Most distributed models of saccade generation used fast efference copy feedback for continuously updating the dynamic motor error (for review, see [13]). In this paper we employ an alternative assumption which is both structurally and computationally simpler to show that collicular dynamic error coding might be realized without feedback but only through the nonlinear, spatio-temporal population dynamics of the collicular neurons. It turns out that different patterns of lateral interconnections within the BN and BUN layers of the motor map are favored by the observed activity pattern.

## 2. Neural Fields and Their Dynamics

A particular useful approach for studying the dynamic behavior of neural populations organized in layers is represented by continuous neural field models [5] which can be described as follows.

Let  $u(\mathbf{x}, t)$  be the average membrane potential of neurons located at position  $\mathbf{x} = (x, y)$  at time  $t$ . The average activity (firing rate) of neurons at  $\mathbf{x}$  at  $t$  is given by the sigmoid-shaped nonlinearity  $f[u(\mathbf{x}, t)]$ , and the average strength of synaptic connections from neurons at position  $\mathbf{x}'$  to those at position  $\mathbf{x}$  by  $w(\mathbf{x}, \mathbf{x}')$ . For homogeneous fields  $w(\mathbf{x}, \mathbf{x}') = w(|\mathbf{x} - \mathbf{x}'|)$  holds. With  $u_0$  the global threshold of the field and  $s(\mathbf{x}, t)$  the intensity of applied stimulus from the outside of the field to the neurons at position  $\mathbf{x}$ , the neural field equation reads

$$\tau \frac{\partial u(\mathbf{x}, t)}{\partial t} = -u(\mathbf{x}, t) + \iint_{\mathcal{R}^2} w(\mathbf{x}, \mathbf{x}') f[u(\mathbf{x}', t)] d\mathbf{x}' - u_0 + s(\mathbf{x}, t), \quad (1)$$

which is the 2-dimensional generalization of Amari's equation [1].

For fields of lateral-inhibition type, excitatory connections dominate for proximal neurons and inhibitory connections dominate at greater distances, described e.g. by a radially symmetrical weighting function of on-center off-surround type which can be modeled by a difference of Gaussians,

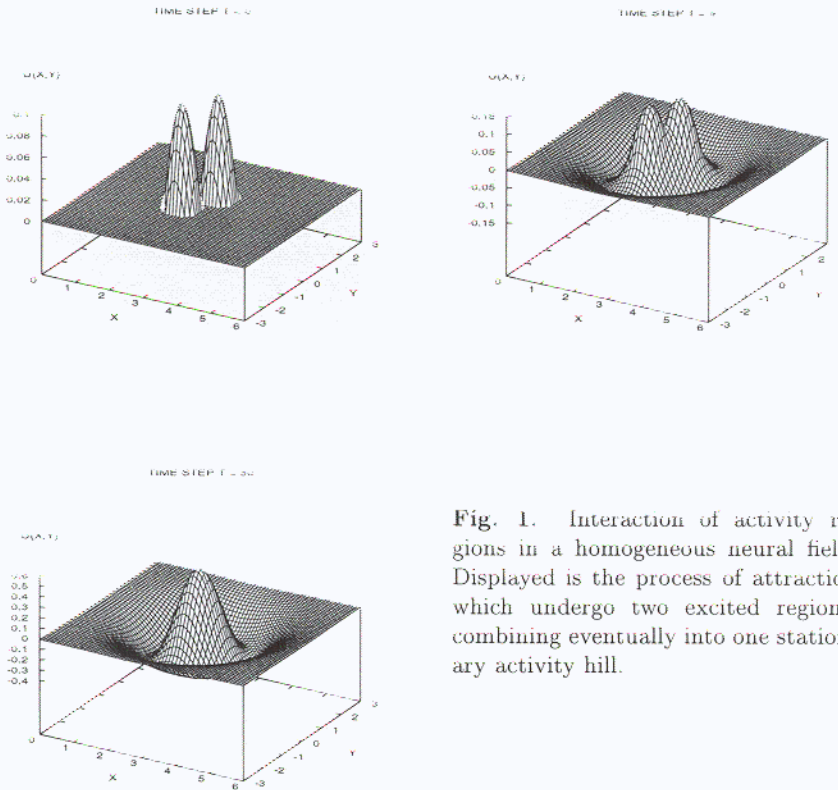
$$w(\mathbf{x} - \mathbf{x}') = g_e \cdot \exp\left(-\left(\frac{\mathbf{x} - \mathbf{x}'}{\sigma_e}\right)^2\right) - g_i \cdot \exp\left(-\left(\frac{\mathbf{x} - \mathbf{x}'}{\sigma_i}\right)^2\right) \quad (2)$$

where  $g_e$  and  $\sigma_e$  are the height and width of the excitatory center and  $g_i$  and  $\sigma_i$  are the corresponding values for the inhibitory surround.

A categorization of the dynamics of *1-dimensional fields* has been provided (see [1] for details). In the case of *2-dimensional neural fields*, this categorization also holds but additional types appear. In single-layer fields, five types of dynamics were proved to exist, which are in general multi-stable and depend on the parameters of the lateral connectivity scheme. Some fields have the ability of keeping a localized excitation pattern at the position where a stimulus arrived, even after it disappeared. This can be related to short-term memory. Interaction of excitation patterns is also possible: two excited regions may attract each other, combining into one local excitation (Fig. 1). In other cases they can repel each other, or coexist independently.

Neural wave patterns include standing, traveling and rotating activity waves, depending on the relative spatial extent of excitatory and inhibitory connectivity. We note that 1-dimensional trajectories of activity hills as observed in the motor map of SC cannot appear in *continuous* 2-dimensional neural fields. This follows from general results on the dynamics of active media (of which neural fields are special cases), saying that in continuous (whether homogeneous or not) active media propagation of excitation is independent on direction

(Keener, 1988; Mikhailov, 1990). In *discrete* active media, however, the situation changes: a *discrete* field model with space-variant, asymmetrical weighting functions exhibits dynamic behavior which corresponds to 1-dimensional trajectories of activity hills. This means, these hills fail to spread laterally to excite the adjacent field regions, if the asymmetry of the weighting function is strong enough [2, 10].



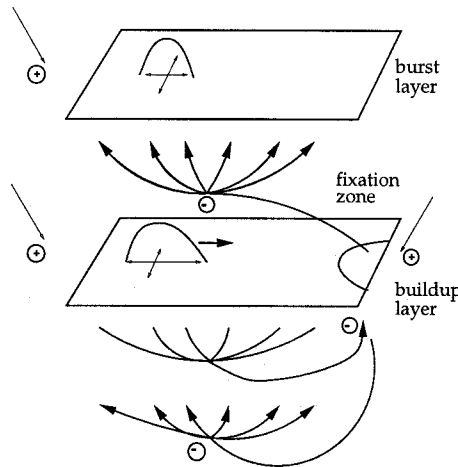
**Fig. 1.** Interaction of activity regions in a homogeneous neural field. Displayed is the process of attraction which undergo two excited regions, combining eventually into one stationary activity hill.

Thus, the field model, Eqn. (1), was endowed with rotationally asymmetric, space-variant weighting functions  $w(\mathbf{x}, \mathbf{x}')$  described as a difference of 2-dimensional Gaussian functions. The weighting function  $w(\mathbf{x}, \mathbf{x}')$  is given in normal form by

$$\begin{aligned}
 w(\mathbf{x}, \mathbf{0}) = & g_c \cdot \exp\left(-\left(\frac{x}{\sigma_{e_x}}\right)^2 - \left(\frac{y}{\sigma_{e_y}}\right)^2\right) \\
 & - g_i \cdot \exp\left(-\left(\frac{x}{\sigma_{i_x}}\right)^2 - \left(\frac{y}{\sigma_{i_y}}\right)^2\right) \quad (3)
 \end{aligned}$$

where  $\mathbf{x} = (x, y)$ .  $g_c$ ,  $\sigma_{e_x}$  and  $\sigma_{e_y}$  are the height,  $x$ -axis width and  $y$ -axis

width of the excitatory center, and  $g_i$ ,  $\sigma_{i_x}$  and  $\sigma_{i_y}$  are the corresponding values for the inhibitory surround. In addition, the major semi-axes of the elliptical isoefficiency contours, described by  $\sigma_{e_x}$  and  $\sigma_{e_y}$ , differed for the half-planes  $x < 0$  and  $x > 0$  which was characterized by the compression factor,  $\kappa$ .



**Fig. 2.** Scheme of the double-layer neural field model. + excitatory connections, - inhibitory connections,  $\searrow$  input from cortical regions.

### 3. Neural Field Model of SC Motor Map

The computational structure of the proposed model is shown in Fig. 2. The model has two neural layers, a BN layer and BUN layer. At the rostral end of the buildup layer, a fixation zone is located. According to the findings of [6, 7], the interaction between these three model compartments has been specified as follows. During fixation, both the BNs and the BUNs are inhibited by the FNs. Afferent input from cortical areas signals the location of a selected target on the BN and BUN layers, and generates an activity switch from the FNs to the BNs and the BUNs.

The two layers have been modeled by a 2-dimensional double-layer neural field, Eqs. (1)-(3). In the simulations, the neural field model was represented by a two-layer grid, where all the neurons of the grid had a step transfer function  $f$ .

#### 3.1. BN layer

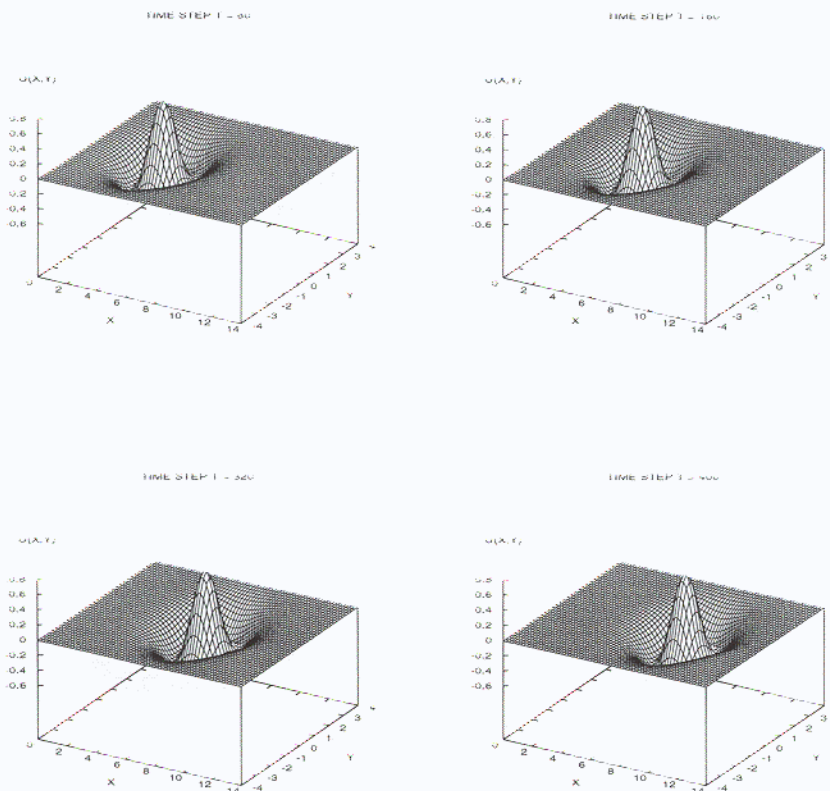
The BN layer has been modeled by a homogeneous neural field, Eqs. (1), (2). The parameters of the connectivity function, Eq. (2), were chosen to obtain the stable solution corresponding to the localized excitation.

#### 3.2. Buildup layer

There is evidence that space-variance occurs in the internal collicular processing. It has been shown that MFs of BUNs typically have a skewed (asymmet-

rical) sensitivity profile [8, 7] which suggests that the strengths of the lateral connections depend on both input and output site rather than on their mere difference.

We used this evidence to model the BUN layer of the collicular motor map by a inhomogeneous neural field, Eqs. (1), (3). Space-variant processing in the model has been realized through the asymmetrical center and surround structure of the weighting function described by Eq.(3) and through the radial organization of the weighting functions, in accordance with the radially organized asymmetry of MFs found in collicular neurons [8].



**Fig. 3.** Shift of activity in the BUN model layer. The BUN layer was modeled by a 70x30 grid. Starting from initial location ( , ), the activity hill moves to the fixation zone with the center ( , ) at the rostral pole of the layer.

As the initial state we chose a localized excitation on the grid that eventually developed into a hill of activity on the mapped field. The localized excitation had a Gaussian shape with maximum  $u = 1.0$ . We run a series of simulations, placing the activity hill in randomly selected locations of the field (Fig. 3).

The simulated pattern of activity in the neural field model showed a clear

anisotropy, resulting from the space-variant coupling of the neurons. The direction of movement was determined by the orientation of the steeper decaying flank of the weighting function defined by  $\kappa$ . The asymmetrical, radially oriented weighting functions caused the hill to move towards the fixation zone where it stopped and finally decayed (see [9, 10] for details).

## 4. Conclusions

In this paper we proposed a model of the spatio-temporal dynamics in the motor map of the SC. We based the model on some high-level computing principles governing saccadic eye movement control, i.e. neural mapping, population coding and space-variant processing in layered systems.

The model relates microscopic data on lateral connectivity within neural layers and emergent dynamic patterns of activity in these layers. For the BN layer we employed a homogeneous lateral coupling structure enabling sustained activity hills. With this behaviour, the BN layer represents a spatial short-term memory storing the target position in retinotopic coordinates.

On the other hand, the BUN layer realizes a form of neural representation known as dynamic memory. Due to the inhomogeneous lateral coupling structure, an activity hill travels from its starting point to the fixation zone while its momentary position codes the remaining motor error. Thus, dynamic error coding is realized through the attractor dynamic in the BUN layer, without any efference copy feedback to this layer. In the case of simple saccades considered here there is also no need for efference copy feedback to the BN layer. However, in situations requiring coordinate transformations (double saccades, sequences, eye-head movements), an eye position feedback seems indispensable. The BN layer as part of the saccade system responsible for target selection and memorizing then will be involved in this feedback loop while the BUN layer need not.

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